

ON THE BRAZILIAN SPECIES IN THE *ACMAEA SUBRUGOSA* COMPLEX
(GASTROPODA: PROSOBRANCHIA: PATELLACEA)

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ABSTRACT

The marine limpets *Acmaea subrugosa* d'Orbigny, 1841, *A. noronhensis* E. A. Smith, 1890, and *A. marcusii* sp. n., are described. The first is recorded from the mainland coast of Brazil, from Alagoas to Rio Grande do Sul, and from Uruguay, the second from the Island of Fernando de Noronha and the third from the Island of Trindade. They cannot consistently be distinguished by their shells. However, there are differences in mandible (Figs. 9-11), radula (Figs. 12-14), course of the intestine (Figs. 15-17) and some peripheral nerves.

In this paper the known Brazilian species of the genus *Acmaea* Eschscholtz, 1833 are described comparatively: *A. subrugosa* d'Orbigny, 1841 (p 140), *A. noronhensis* E. A. Smith, 1890 (p 495) and *A. marcusii* sp. n. Caribbean species occurring sporadically in Brazil are excluded.

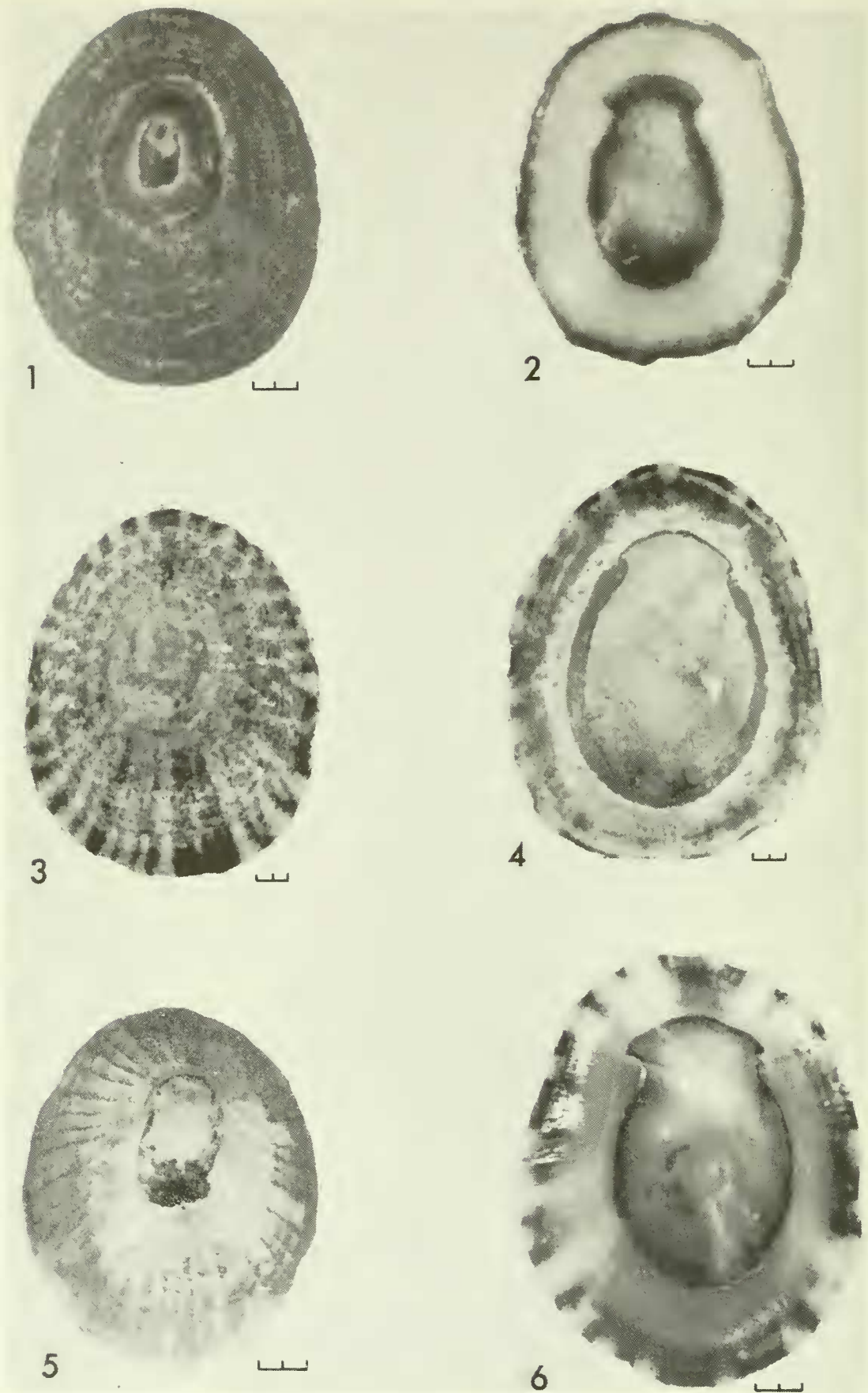
A. subrugosa is widely distributed on the Brazilian coast, from Alagoas (information kindly sent by Dr. Eliezer Rios, Museu Oceanográfico do Rio Grande, Rio Grande do Sul) south to Rio Grande do Sul, and occurs also in Uruguay (Barattini, 1951: 191). In the literature, *A. subrugosa*, has been identified only by shell characters. The limpets on the coast of São Paulo (Ubatuba-Peroibe) are all *A. subrugosa*, and I have studied its soft anatomy. *A. noronhensis* is restricted to the Island of Fernando de Noronha (3° 40' S, 32° 25' W), and *A. marcusii* to the Island of Trindade (20° 30' S, 29° 22' W).

I have studied 30 specimens of *A. subrugosa*, all from the coast of São Paulo. Thanks to Prof. Hugo de Souza Lopes (Instituto Oswaldo Cruz, Rio de Janeiro), who kindly sent me 10 specimens from Fernando de Noronha (Souza

Lopes & Alvarenga, 1955: 161-162), I could also study the anatomy of *A. noronhensis*. And thanks to Dr. Arnaldo C. dos Santos Coelho (Museu Nacional, Rio de Janeiro), I received 32 limpets of the new species collected by Mr. J. Becker. Of these, I have studied 9 anatomically. I am indebted to Dr. Paulo Vanzolini and Lic. José Luiz Moreira Leme for permission to photograph shells of *A. noronhensis* in the collection of the Departamento de Zoologia, Secretaria da Agricultura do Estado de São Paulo, and to Profs. Drs. Eveline and Ernst Marcus for advice.

SOME ECOLOGICAL DATA ON
ACMAEA SUBRUGOSA

This eurytopic species lives in the intermediate and high intertidal areas. It inhabits rocks, especially sides sheltered against large waves, feeding on microscopic algae. It is mainly accompanied by barnacles (*Tetraclita*), the prosobranchs *Fissurella* and *Diodora*, and the pulmonate *Siphonaria hispida*. Littorinidae live among *Acmaea* and farther above. Gofferjé (1950: 230) found *A. subrugosa* on *Mytilus*, *Ostrea*



FIGS. 1-6. Shells of *Acmaea*: 1, 2, *A. noronhensis*; 3, 4, *A. subrugosa*; 5, 6, *A. marcusii*. Each scale line is 2 mm long.

and *Thais*. Its movements are slight and slow, usually in irregular paths. It rarely moves in circles and comes back to its original place. Other species of *Acmaea* have a pronounced homing instinct (Villemé & Groody, 1940: 201; Hewatt, 1940: 206). When disturbed, *A. subrugosa* adheres firmly to the substrate.

MORPHOLOGICAL OBSERVATIONS

The following description applies to all 3 Brazilian species. When a given characteristic is not shared by them it is explicitly referred to the respective species.

The shell (Figs. 1-6)

The shell is solid, patelliform in the 3 species, broader behind than in front and more produced at the ends. Only the ends touch the substrate, and circulation of water or air is possible through the cleft on each side between the rock and the lateral margin. The apex is directed forward (rather upward in young specimens). The average dimensions of full-grown specimens are as follow (length, greatest breadth and height, respectively): *A. subrugosa* (30 shells): 20 mm, 16.7 mm, 7.5 mm; *A. noronhensis* (20 shells): 16.5 mm, 13 mm, 6 mm; *A. marcusii* (9 shells): 18.5 mm, 15 mm, 7.3 mm. *A. marcusii* is intermediate in size between the other two. Young specimens of *A. subrugosa* are proportionally higher because shells over 5-6 mm in length grow more in length and breadth than in height. The apical periostracum is usually intact in *A. subrugosa* and *A. noronhensis*, and eroded in *A. marcusii*.

The margin is oval in outline, smooth or slightly crenulate in *A. subrugosa*. There are inconspicuous axial ribs in *A. subrugosa* crossed by thin growth lines, and high narrow radial striae in *A. noronhensis* and *A. marcusii* (fainter in the latter).

The shell of *A. subrugosa* has irregularly disposed radial white and dark

bands, the dark bands sometimes bifurcating near the periphery; some specimens show a broad axial dark band in front and a still broader one behind. More frequently, these bands are found only on the inner surface in the 3 species.

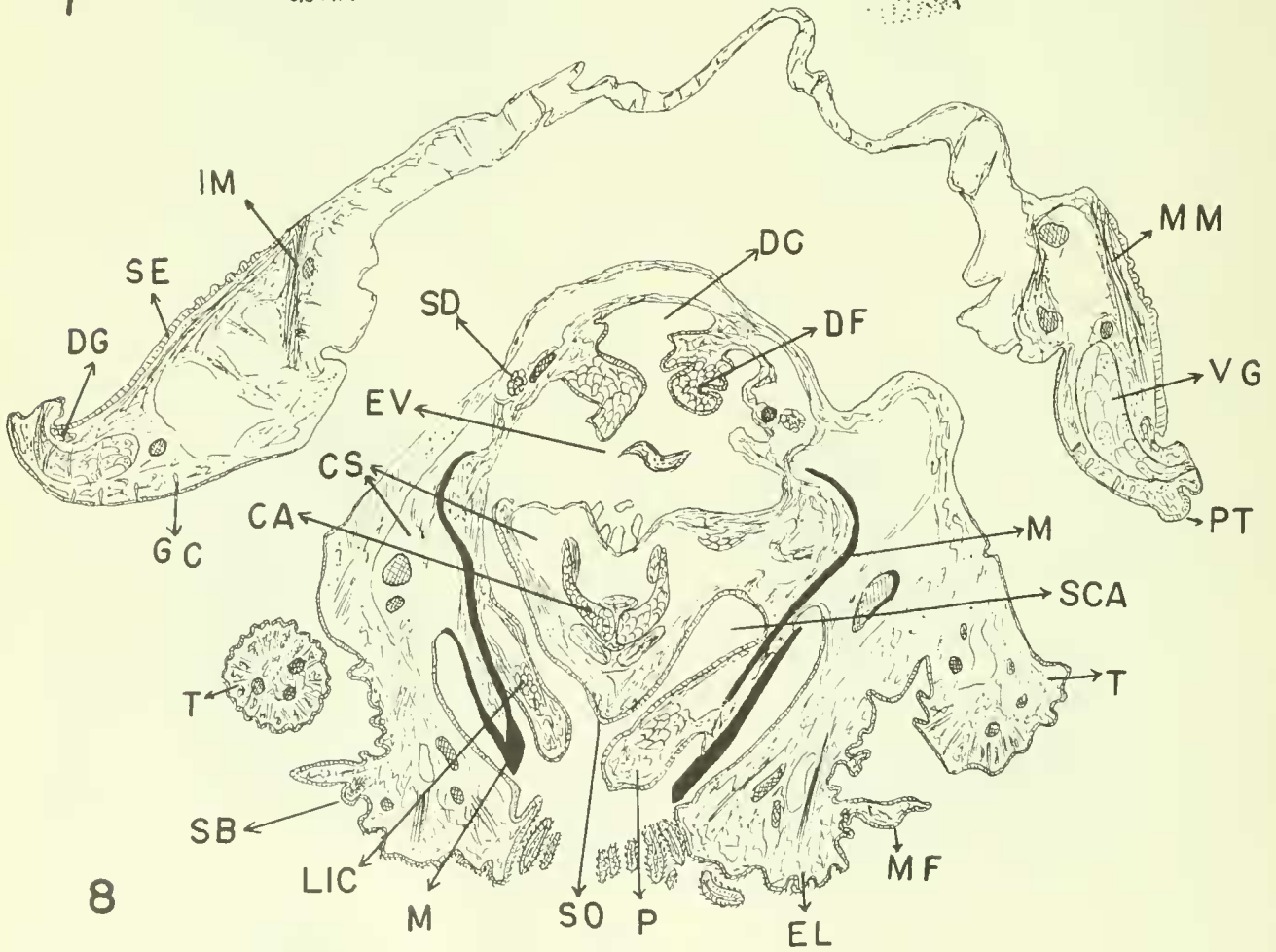
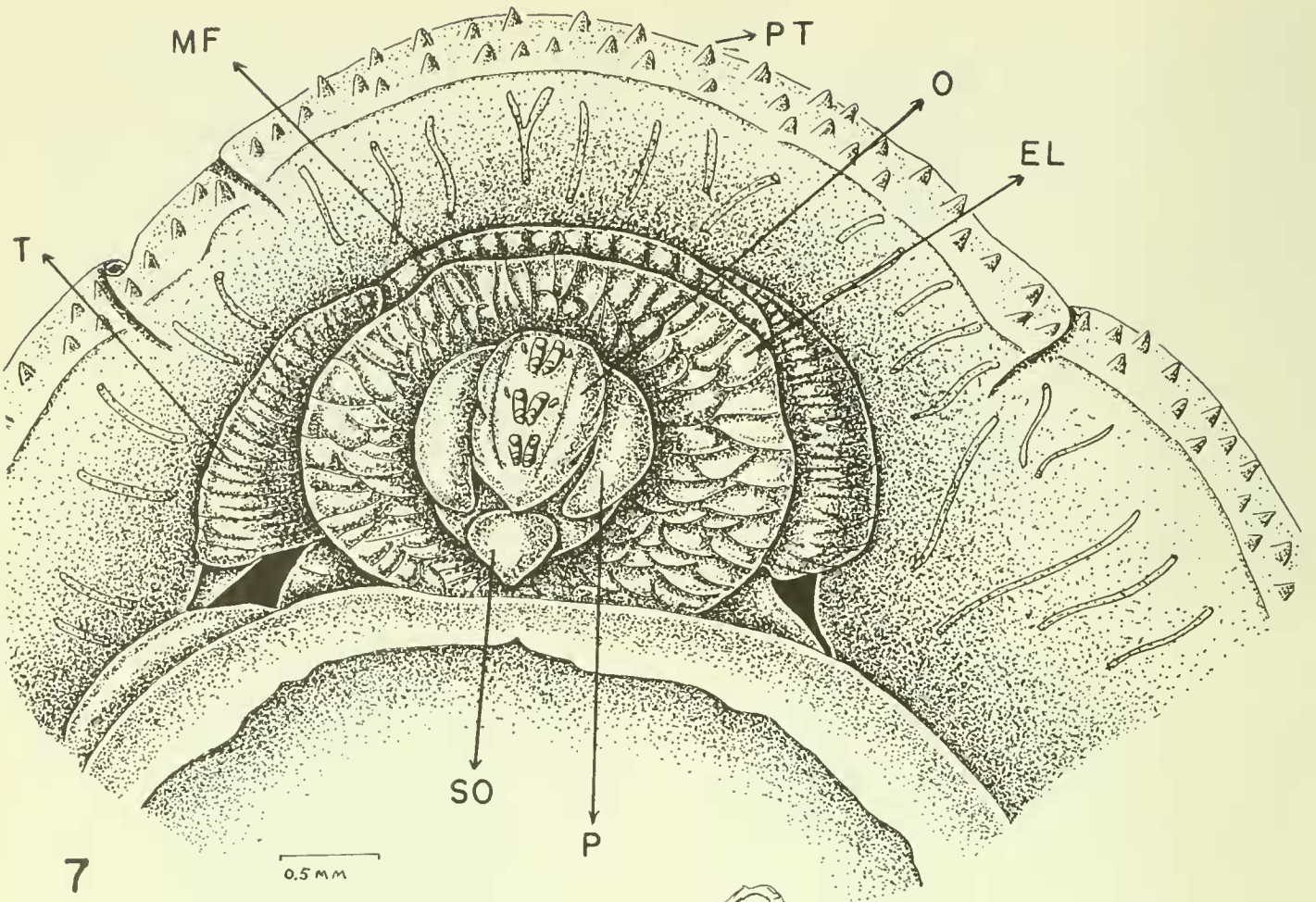
The shell of *A. noronhensis* is darker than that of *A. subrugosa*, has more slender and higher radial striae, and has a dark inner margin, as already noted by Smith (1890).

In *A. marcusii* the general external color is light brown, sometimes with white axial bands. As in *A. subrugosa*, there is a zone of radial dark brown bands along the inner margin, sometimes so numerous that they form a dark, almost continuous band as in *A. noronhensis*.

According to Souza Lopes & Alvarenga (1955: 162), the shell of *A. noronhensis* has a dark, sometimes almost black surface, contrasting with white radial bands which end at the margin or do not attain it, and also shows high thin, very distinctly black radial striae. Both characters occur in *A. marcusii* and *A. subrugosa* too, less frequently in the latter.

The scar of the columellar muscle is light to dark brown in *A. subrugosa*, and looks like a horseshoe opening forward, with the extremities joined by a narrower band resulting from the insertion of mantle muscles. The scar surrounds a surface that is generally leaden, sometimes either rather blackish or white. A dark brown band runs subterminally along the inner margin, and sends out peripheral rays of its own color. The area between the band and the scar of the columellar muscle is whitish, contrasting with the dim inner area. The reverse, however, may occur, or both areas may show the same hue, cream white to leaden. Such variability renders it difficult to separate *A. subrugosa* from the other 2 by these characters.

The columellar impression is nacreous and little perceptible in *A. noronhensis*, and is accompanied inwardly by a large band which encircles a usually



FIGS. 7, 8. Head region of *Aemaea subrugosa*: 7, Ventral anterior view during radular scraping; 8, cross-section.

LIST OF ABBREVIATIONS

AB - afferent branchial vessel	MV - mantle vein
AC - abfrontal cilia	NS - neural sinus
AFS - afferent sinus	NT - transverse connection between posterior pallial nerves
AL - anterior labial nerve	O - odontophore
AP - anterior pedal nerve	ON - optic nerve
BG - buccal ganglion	P - palp
BN - branchial nerve	PA - proventricular aperture
CA - anterior cartilage	PD - pedal ganglion
CC - cerebral commissure	PG - pleural ganglion
CG - cerebral ganglion	PL - posterior labial nerve
CIN - circumpallial nerve	PN - pedal nerve cord
CIS - circumpallial sinus	PPA - posterior pedal artery
CM - columellar muscle	PS - median pedal sinus
CN - columellar nerve	PT - pallial tentacles
CPD - cerebropedal connective	PV - proventriculus
CPL - cerebropleural connective	PVL - perivisceral lacunae
CS - cephalic sinus	RA - right anterior pallial nerve
DC - dorsal food canal	RK - right kidney
DF - dorsal folds of pharynx	RN - right nephridial nerve
DG - dorsal glands	RO - right osphradial ganglion
DGD - digestive gland duct	RP - right posterior pallial nerve
EB - efferent branchial vessel	S - stomach
EFS - efferent sinus	SAP - posterior sorting area
EL - external lip	SB - sensory button
EN - esophageal nerve	SC - sensory cell
ES - esophagus	SCA - subradular cavity
EV - esophageal valve	SD - salivary ducts
FC - frontal cilia	SE - sensorial epithelium
GC - subepithelial glandular cells	SG - subintestinal ganglion
GO - gonad	SGL - sole glands
IM - internal pallial muscle	SO - subradular organ
LA - left anterior pallial nerve	SPG - supraintestinal ganglion
LC - lateral cilia	ST - statocyst
LF - longitudinal fold	SU - supporting cells
LG - labial ganlion	T - cephalic tentacle
LIC - lateral inferior cartilage	TC - terminal cilia
LN - left nephridial nerve	TF - band of transverse folds
LO - left osphradial ganglion	TN - tentacular nerve
LP - left posterior pallial nerve	UB - unicellular trabeculae
LS - lateral pedal sinus	UG - unicellular granular gland
LSC - lateral superior cartilage	VG - ventral glands
M - mandibular plate	VIG - visceral ganglion
MF - membranous fringe	VN - visceral nerve
MM - mantle muscle	

leaden area.

In *A. marcusii* the scar is the same as in *A. noronhensis*, and is accompanied by a narrow dark brown band that limits a leaden area which is lighter than in *A. noronhensis* and contrasts with the whitish peripheral area.

Head

In dorsal view the head in the 3 species

resembles a truncated cone directed forward and sharply bent downward in front so that the mouth is ventral.

The papillose external lips (Fig. 7, EL) are shaped like a horseshoe opening backward and surrounded by a furrowed membranous fringe (MF). The oval contour of the mouth leaves free the inner lip or palps and, at the sides, the mandibular plate. In some anesthetized speci-

mens of *A. subrugosa* the extroverted odontophore (O) is seen between the palps (P), and the heart-shaped subradular organ (SO) lies under it. The rather distensible cephalic tentacles (T) lie on each side of the head. Their thickened bases bear the small dark eyes.

Foot and columellar muscle

The oval foot has a well-defined margin which separates the under from the lateral surfaces. Its muscles (Fig. 27) consist chiefly of dorsoventral fibers, continuous with those of the columellar muscle, and of less developed oblique and horizontal ones. The latter are peripheral and form a thin muscle layer bounding the connective tissue which in the sole contains many blood lacunae and gland cells.

The high ciliary epithelium of the sole is pierced by the canals of the sole glands (Fig. 27, SGL). These unicellular glands are mainly mucous and most concentrated in the anterior and lateral parts of the foot, scarce in the center and behind. Other unicellular subepithelial glands (UG), whose secretion is chiefly granular, open on the lower parts of the lateral walls.

The diameter of the animal gradually decreases from the sole upward, so that the area where the columellar muscle inserts corresponds to the smallest diameter of the body.

The insertion of the columellar muscle (Figs. 23, 26, CM) resembles a horseshoe with widened ends. Removing the shell, one can see that apically the muscle is not a continuous band, but is divided into bundles separated by the lateral sinus of the foot. The sinuses are more or less visible, depending on whether they are full of blood or empty. The number of muscle bundles is variable, there being usually 6 on each side in *A. subrugosa* and *A. marcusii*, and 7 in *A. noronhensis*. The columellar muscle (Fig. 27, CM) is essentially constituted of dorsoventral fibers which integrate the lower part of the foot; they are intercrossed with longitudinal

fibers sometimes disposed in small bundles. There are very few horizontal fibers and these are near the apex, where the numerous dorsoventral ones branch off. The adhesion of the shell is effected by an epithelium of cubic cells (of 8.5μ average height in *A. subrugosa*) with indistinct cell boundaries; fibrils run through them, as in *Tegula viridula* (Righi, in press) and *Acroloxus lacustris* (Hubendick, 1958: 31).

Pallial complex

As in other Patellacea, the pallial cavity comprises a groove around the whole foot, besides the nuchal cavity behind the head.

The nuchal cavity is laterally limited by the anterior extremities of the columellar muscle. On each side of its floor lies a yellowish osphradium, semilunar in *A. subrugosa*, obliquely lengthened in *A. marcusii* and smaller and irregular in *A. noronhensis*. On the ceiling of the right posterior region of the cavity runs the rectum with the anal opening flanked by 2 nephridiopores. The rectum projects into the nuchal cavity, farther in *A. noronhensis* than in *A. subrugosa*; in *A. marcusii* it opens just over the right osphradium. On the left side the bipectinate gill hangs from the ceiling with a slight inclination, so that the afferent margin is somewhat dorsal. There are neither afferent and efferent membranes, nor skeletal bands for support. The branchial musculature is chiefly longitudinal, disposed as a pair of lateral bands protruding into the cavity of the 2 sinuses and especially developed along the efferent one.

There are up to about 70 ctenidial lamellae on each side in *A. subrugosa* and a few more in *A. noronhensis* and *A. marcusii*. They form broad triangles (Fig. 18), whose longer side is attached to the support. Afferent and efferent sinuses in the lamellae (Fig. 20, AFS, EFS); are at the margins, and join a big lacuna. The latter occupies the entire lamella and is crossed by

thin unicellular trabeculae (UB) which maintain the walls in position. In *A. subrugosa* the coating cubic epithelium bears short cilia over the whole surface of the lamellae, and the frontal and abfrontal cilia are also little developed. The lateral strong cilia (LC) and the terminal ones (Fig. 18, TC) are on a narrow band of cylindrical cells. The thin basement membrane is sometimes absent. There is no hypobranchial gland.

The muscular system of the mantle is most developed in the proximal region. It consists of dorsal fibers of the mantle muscle (Figs. 8 and 27, MM) and oblique ones, the internal pallial muscle (IM) in the septum separating the venous from the arterial system. These fibers join at the bases, some adhering to the columellar muscle and others to the shell beside it. Contraction of these fibers retracts the mantle. There are also longitudinal and transverse fibers which bring about the shortening and thinning of the mantle.

Outside the circumpallial sinus is the glandular area of the mantle. Two kinds of glands are recognizable; the more evident ventral glands (VG) are large mucous granular cells which narrow toward the periphery. Their thin ducts open isolated among the epithelial cells, mainly in the region ventral to a narrow furrow around the mantle. In young limpets these cells form a continuous strip; in adults they form groups, separated by connective tissue and muscle fibers which enclose the body of the gland. The dorsal glands (DG) are the second kind of gland, inconspicuous small nodules of intensely stainable pear-shaped cells which open into the mantle furrow. In adults, large gland cells (GC) descend into the connective tissue and open on the ventral face. According to Fretter & Graham (1954: 579; 1962: 119) those glands are repugnatorial.

The dorsal epithelium of the mantle (SE) is much higher than the ventral one, and more developed in *A. noronhensis* than in *A. subrugosa* and *A. marcusii*.

It consists of cylindrical cells with brown apical granules, intermingled with sensory cells. Further sensorial structures are the pallial tentacles (Fig. 8, PT).

Circulation of respiratory water and elimination of particles in *A. subrugosa* are performed in the same way as described in *A. testudinalis* and *A. virginea* by Yonge (1947: 465; 1962: 120, Fig. 1A); *A. subrugosa* agrees with *Lottia gigantea* (Abbott, 1956: 86, Fig. B) in the absence of an axial ciliary current along the efferent margin of the ctenidium. Particles which pass between the ctenidial lamellae or along their contour by action of the frontal, terminal and abfrontal cilia are heaped up on the afferent margin. They are carried over the floor of the nuchal cavity by the branchial cilia or movements of the ctenidium, then conveyed toward the right by strong ciliary currents and backward into the pallial groove. I did not find any ciliation on the pallial tentacles. During low tide the columellar muscle is partly relaxed, and, owing to the previously mentioned shell configuration, a narrow gap remains between the shell and the rock, allowing for the passage of air which diffuses into the residual water in the nuchal cavity and the pallial groove, making aerial breathing possible.

Alimentary tract

1. Buccal cavity

The buccal opening (Fig. 7) is broader than high. It opens ventrally when the head is in its normal position.

The papillae that cover the lips are chiefly constituted of connective tissue. Their epithelium has prismatic cells with basal, longish and densely chromatic nuclei and homogenous plasma. It is coated with a thick cuticle in which denticles are recognizable. There are simple thorny projections of the cuticle as in *Acmaea digitalis* (Thiele, 1902: 338, Fig. 105). They probably retain alimentary particles, but do not scrape

growth from rocks as Fisher assumed for *Lottia gigantea* (1904: 6).

The membranous fringe (Figs. 7 and 8, MF) surrounding the lips is constituted of connective tissue crossed by numerous blood lacunae and few muscular fibers. The cubic epithelium of the fringe is continuous with that of the head. It is separated from the lips by a deep furrow containing sensory buttons in *A. subrugosa* and *A. marcusii* (Fig. 8, SB). The buttons are supplied with nerves from the labial ganglia. They are essentially connective structures, traversed by weak muscular bands. Their epithelium is formed by cells up to 15.3μ in height with basal oval nuclei and covered with a thin cuticle pierced by numerous cilia. Among these supporting cells there are neuroepithelial ones with spindle-shaped, intensely staining nuclei. The epithelium of the furrow around the button consists mostly of mucous glands and of a few granular ones.

The buccal opening leads into a spacious oral cavity containing the odontophore, the subradular organ, the palps and the mandibular plate.

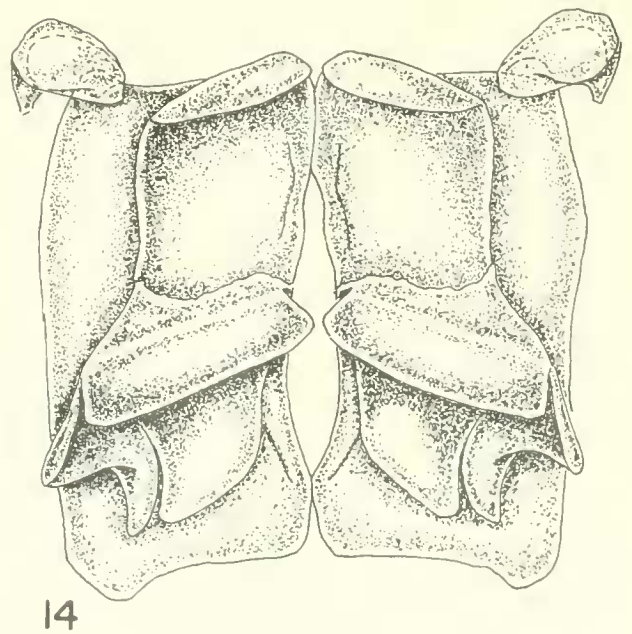
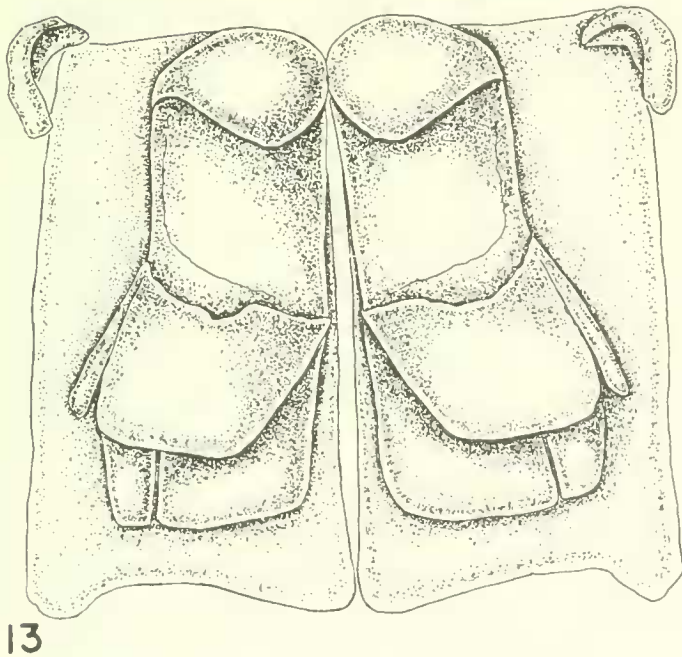
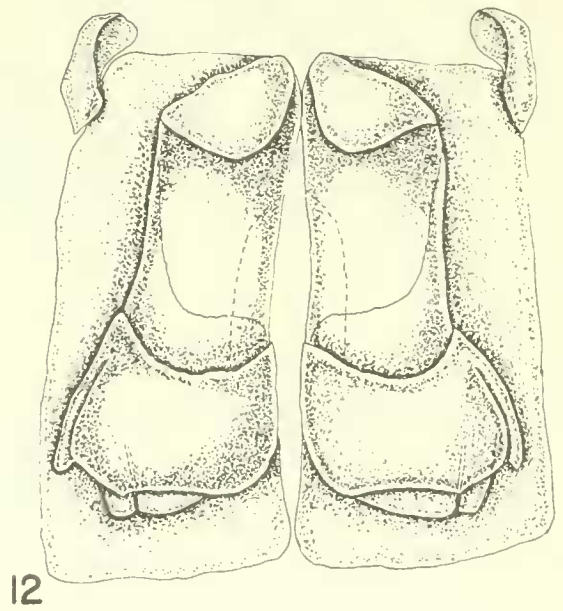
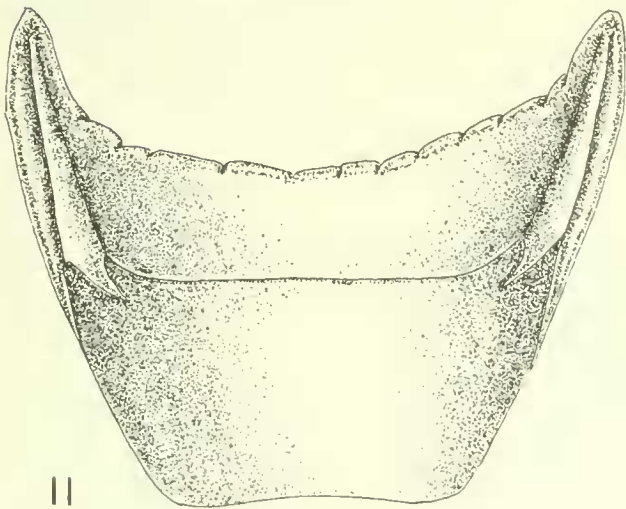
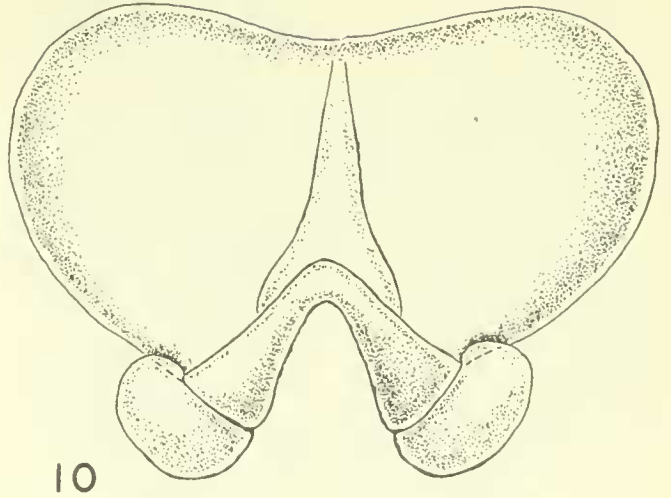
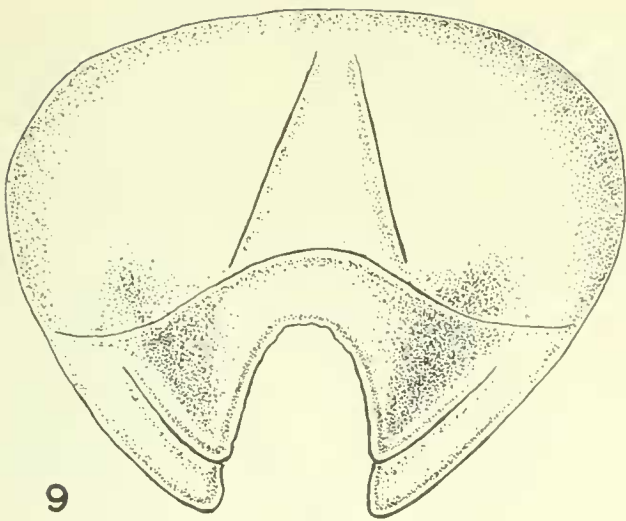
The palps (Figs. 7 and 8, P) are visible through the mouth as 2 triangular masses. When the limpet feeds they are expanded and located on the sides of the odontophore. They are mainly formed of connective tissue with big blood lacunae and crossed muscle fibers, and rest on the lateral inferior cartilages (Fig. 8, LIC). The epithelium is cylindrical, ciliated in the center and provided with a thick denticulate cuticle on the sides. On the inner wall, which forms the anterior limit of the subradular cavity, there is a thick layer of conchiolin which continues into the greater part of the furrow running along the inner side of the external lips. The opposite wall is in close contact with the mandibular plate.

The subradular cavity (Fig. 8, SCA) is limited dorsally by the buccal mass and ventrally by the floor of the oral cavity of which it is a diverticulum. The

lateral inferior cartilages of the odontophore accompany this canoe-shaped cavity. The coating epithelium is highest below, between the cartilages, where the conchiolin layer continues. Some glandular cells are found on the sides and above.

The subradular organ (Figs. 7 and 8, SO) is located under the odontophore, and looks like an isosceles triangle in cross-section. The anterior end has a deep notch with high cylindrical epithelium. Its cells produce a thick cuticular layer continuous with the basal membrane of the radula. On the median and posterior areas the coating of the organ shows rounded denticles, finger-shaped in *A. marcusii*, much smaller than those of the lips, as in *Acmaea digitalis* (Thiele, 1902: 336). In this region, many longitudinal furrows are disposed symmetrically in *A. subrugosa*. The subradular organ, roomy in its center, contains longitudinal and transverse muscular bands, the former being more numerous. When the animal scrapes, this organ is extroverted and greatly increases in size by accumulation of blood. Sensory cells like those found in the subradular organ of *Acmaea virginea* and *A. testudinalis* (Willcox, 1901: 624) do not occur.

The single jaw or mandible (Figs. 9-11) probably results from median fusion of a pair, as in most prosobranchs. Two wings, the anterior smaller than the posterior one, are quite distinct on each side of the mandible of *A. subrugosa*. The color is light brown for the most part and dull brown on the thick anterior end. The latter (Fig. 8, M) projects into the buccal cavity between the palps and the external lips; inwards, it reaches the dorsal folds of the pharynx. In *A. noronhensis* it is canoe-shaped, with a dark brown broader and thicker anterior portion. The irregularity of its margin is due to friction against the substrate. Its great thickness makes histological sections of the head difficult. The slender jaw of *A. marcusii* is narrow and strongly concave



FIGS. 9-14. Jaw in *Acmaea*: 9, *A. marcusii*; 10, *A. subrugosa*; 11, *A. noronhensis*.
 Radular row in *Acmaea*: 12, *A. subrugosa*; 13, *A. noronhensis*; 14, *A. marcusii*.

anteriorly, and widened and flattened posteriorly. The thicker anterior third is demarcated by a transverse furrow; equally thick is the concave median region opposite the radula. The mandible of the 3 species has no rod-like structures. Many odontophore muscles are joined to the mandible; also the palps, external lips and dorsal folds of the pharynx are attached to it by strong muscular ligaments. When the mandible is everted from the buccal cavity, the dorsal folds of the pharynx are drawn forward, enlarging the food canal and the opening of the ducts of the salivary glands and causing a release of saliva. The enlargement of the food canal causes the entrance of food particles. The mandible does not contribute actively to capture of food; rather, it serves as a support for the anterolateral portion of the cephalic cavity and protects the external lip from damage by the radula.

The odontophore is an oval mass constituted of many muscular bands wrapping 3 pairs of cartilages. The anterior (Fig. 22, CA) and the lateral superior (LSC) cartilages are canoe-shaped. The anterior ones are long, widest in the middle; they diverge backward and have the shape of two little rods. The lateral superior cartilages are disposed as a hood over the anterior ones. The lateral inferior cartilages (Fig. 8 LIC) support the palps and extend along the subradular cavity; few odontophore muscles are fastened to them.

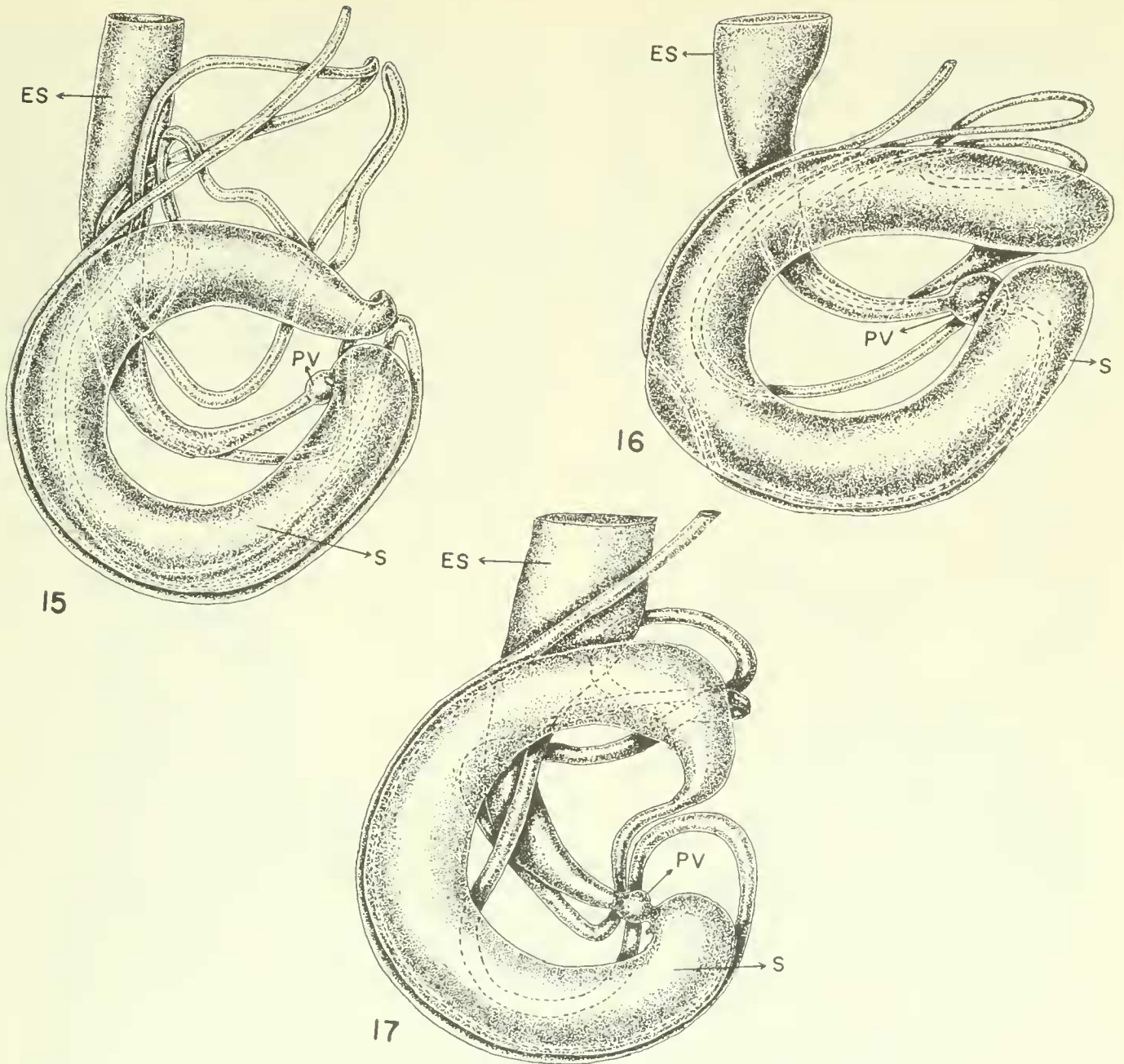
The radula (Figs. 12-14) has the formula 1·3·0·3·1. The lateral teeth are partly coalesced so that they show a common rectangular basal plate. The inner teeth are anterior on the plate and their basal portion narrows anteriorly in *A. subrugosa*; the bases of the long cusps touch one another. The 2 external laterals are posterior on the basal plate. They are partially fused, having a smaller external and a larger inner cusp with a little eccentric point in *A. subrugosa*. In symmetrical teeth their

inner edge is parallel in *A. subrugosa*, divergent in *A. noronhensis* and convergent in *A. marcusii*. The marginals are implanted as 2 small plates on the radular membrane near the external superior corner of the basal plate of the lateral teeth. In *A. noronhensis* the teeth are especially strong.

The radular sheath of *A. subrugosa* and *A. marcusii* is as long as the shell, and one and a half times as long in *A. noronhensis*. In *A. subrugosa* it passes through the cephalic artery, and then extends into the visceral cavity, accompanying the esophagus on the left side; it goes downward and reaches the floor of the cavity, where it is enclosed by the gonad. Then it curls to the right and upward, runs over the proventriculus and goes on forward, attaining the morphologically anterior portion of the stomach, where it bends to the left and ends in a widening. The arrangement of the radular sheath is essentially the same in the other 2 species. In *A. marcusii* an anterior left loop appears a little after its passage through the cephalic artery; in one specimen the loop was on the right.

In the 3 species there is a pair of folds (Fig. 8, DF) on the inner dorso-lateral walls of the pharynx, which continues into the esophagus. Between them runs a deep, large furrow, the dorsal food canal (DC). These folds extend forward to the neighborhood of the palps. They consist of connective tissue which contains unicellular mucous glands opening by long ducts among the epithelial cells. Muscular fibers run along the whole length of the folds. The ducts of the salivary glands open into the anterior region of the food canal, whose cylindrical epithelium is higher and has longer cilia around the opening of these glands.

The esophageal valve (EV) lies in the buccal cavity between the aperture of the radular sheath and the esophageal folds. In *A. subrugosa* it joins the lateral esophageal walls, serving as a ceiling of the radular sheath and as a



FIGS. 15-17. Gut of *Acmaea*: 15, *A. noronhensis*; 16, *A. marcusii*; 17, *A. subrugosa*

floor of the food canal. In *A. marcusii* it is smaller and joins the odontophore laterally, so that it does not abut on the food canal. In both species it consists of few muscular fibers with a big blood lacuna in direct communication with the cephalic sinus.

2. Esophagus

The anterior ventral limit of the esophagus is indicated by the opening of the radular sheath, the dorsal one by an imaginary plane which runs over the odontophore and reaches the opening of the salivary glands (Fretter & Graham,

1962: 207). The esophagus is flattened dorsoventrally. The folds of the food canal (Fig. 8, DF) extend backward and are strongly bent outward; their free margins are dilated by a blood lacuna which also extends backward. Small longitudinal folds appear between the main folds. The epithelium has big cylindrical cells with long cilia in the furrow between the folds. Goblet cells are scanty in front, and common in the middle and posterior parts of the esophagus.

Two ventrolateral folds project into the lumen of the esophagus near the base

of the esophageal valve in *A. subrugosa* and *A. noronhensis*, and farther behind in *A. marcusii*. They approach one another posteriorly, eventually fusing into a bifid ventral fold. Their cylindrical ciliary epithelium is higher on their inner surface. Anterior to the ventral folds there is, in *A. marcusii*, a median longitudinal fold with high glandular cells. The dorsal folds in *A. subrugosa* appear as longitudinal dark bands on the external surface of the esophagus.

The lateral walls of the esophagus form two large pouches (of which the right is larger) at the region where this organ shows a twist of 90°. Numerous transverse septa divide the pouches into smaller ones, whose number increases posteriorly and which are less numerous on the left side. The anterior lateral walls of the esophagus in *A. marcusii* are made up of high mucous cells, probably in compensation for the less developed posterior salivary glands.

The esophagus twists again still farther back, so that the dorsal folds become ventral and the ventral ones dorsal. Its lumen gradually narrows (Figs. 15, 16, 17, ES) and the folds disappear. Then numerous longitudinal folds arise on the whole inner surface. Now the esophagus, which first ran on the left side of the animal, shifts toward the right upper side. Shortly before opening into the stomach, it widens into a little chamber, the proventriculus (PV). Its walls are densely furrowed in *A. subrugosa*, scarcely so in *A. noronhensis* and *A. marcusii*.

3. Stomach

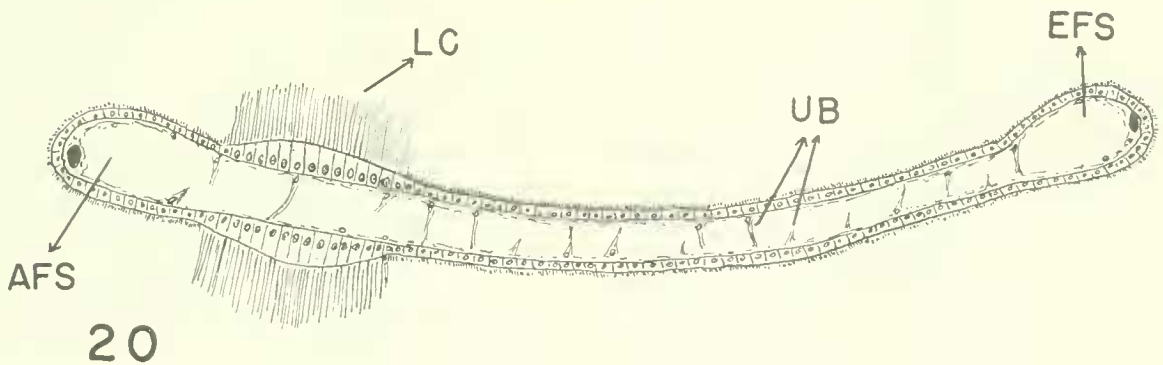
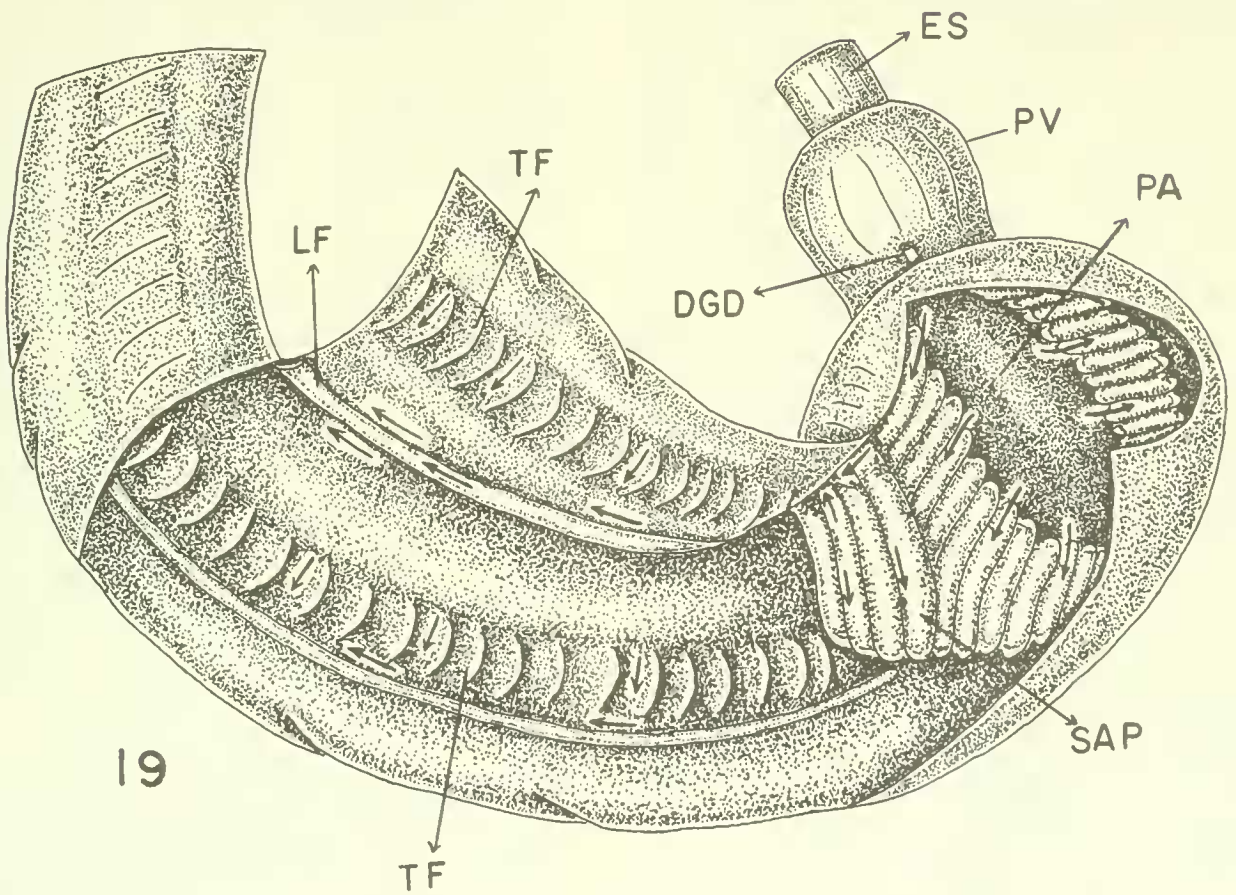
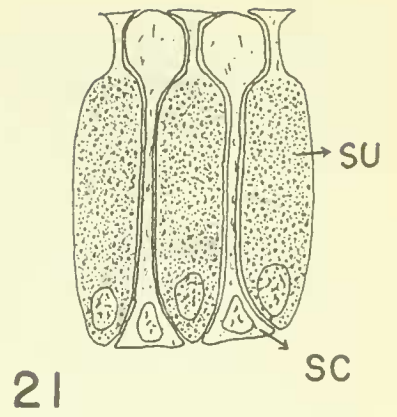
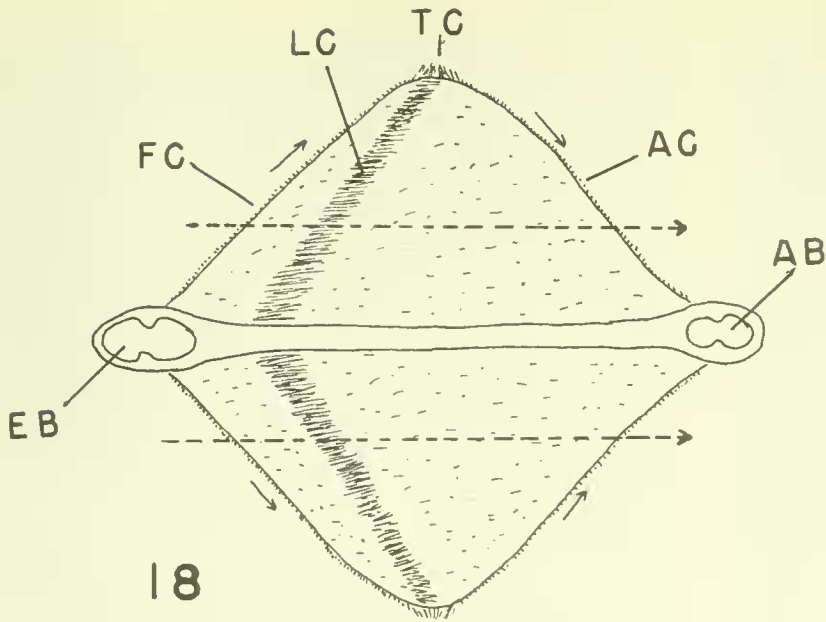
The stomach is separated from the proventriculus by a strong constriction. It begins on the right side (Figs. 15, 16, 17), assumes a circular ascendent path to the left and forward, and then its lumen narrows. It surrounds the dorsalmost part of the digestive gland, which in *A. subrugosa* covers its extremity, leaving a little area visible on the left side when the shell is removed;

in *A. noronhensis* the loop is more closed, and also a little central part is covered by the digestive gland; in *A. marcusii* only its peripheral area is visible. The stomach of *Acmaea* has neither spiral caecum, gastric shield and typhlosoles, nor a style sac or a proto-style. The following observations refer to *A. subrugosa*: The proventricular aperture (Fig. 19, PA) is a wide oval slit with several little folds which continue from the proventriculus into the beginning of the stomach. A little transverse tuck represents a reduced posterior sorting area (SAP), as in *Patella vulgata* (Graham, 1949: 749). On the inner angle of the stomach, where the 2 typhlosoles occur in other Archaeogastropoda, there are some small longitudinal folds, of which the median one is the most evident. In the median region of the stomach these folds are united in a single larger one (LF), which in the pyloric region divides again disorderly and indistinctly. The posterior sorting area continues onto the morphologically dorsal and ventral walls with a band of transverse folds (TF) like that recorded in *Lottia gigantea* (Fisher, 1904: 13). These folds diminish backward and approach the inner angle, those of the ventral band more rapidly. They disappear in the pyloric region, only a small longitudinal fold penetrating into the intestine. The ventral band is accompanied externally by a longitudinal fold.

In the posterior sorting area and in the transversely folded bands, the epithelium is constituted of 60 μ high wedge-shaped cells, wider at the apex, with long cilia. Between these supporting cells there are goblet cells. Backward, the epithelium of the bands is lower and goblet cells are scarce. The remaining gastric wall is formed of cylindrical glandular cells about 20 μ high with short cilia.

The passage from the stomach to the intestine is gradual.

In the 3 species examined, the digestive gland communicates with the



FIGS. 18-21. *Acmaea subrugosa*: 18, Branchial leaflets (solid arrows show ciliary currents; dashed ones, course of water). 19, Dorsal aperture of the stomach; the arrows indicate currents of cilia; 20, Section of branchial leaflet; 21, Cells of retina.

stomach by a single duct (DGD) which opens into the posterior sorting area just over the aperture of the proventriculus. This opening forms a sharp angle, with the inner part directed toward the digestive duct.

The food particles are carried by cilia from the opening of the digestive gland toward the posterior sorting area; ciliation was not found inside the gland. From the posterior sorting area the particles take 3 main directions. The most important is toward the ventral band of transverse folds, whose ciliation directs the particles to the furrow between that band and the previously mentioned longitudinal fold. Along the furrow the particles are wound forward. Few particles are carried from the posterior sorting area to the dorsal band, where a transverse current directs them to the inner angle, whence they are carried forward together with most of the residue from the digestive gland. Some particles go from the posterior sorting area toward the longitudinal fold.

The inner morphology of the stomach of *A. noronhensis* and *A. marcusii* was not studied because in the preserved material it was filled with mucous masses adhering to the walls.

4. Intestine

The complex course of the intestine (Figs. 15, 16, 17) through the digestive gland and the gonad is essentially the same in the 3 species. The intestine is longer and more complex in *A. noronhensis* than in *A. subrugosa* and *A. marcusii*. In the 3 species the rectum has 2 big folds (dorsal and ventral) of connective tissue, which begin a little before it enters the mantle. The walls of the rectum to the right and left of the folds are different. The epithelium of the left wall is up to $6\ \mu$ high, with few but long cilia. High folds occur on the right wall, whose epithelial cells are up to $13.5\ \mu$ high and have many small cilia, and where goblet cells are frequent. The limit between the 2 types of epithelium lies at the

apex of the 2 big folds. In the mantle, the rectum bends toward the left at a right angle, so that the dorsal and ventral folds become lateral near the anus.

The inner structure of the rectum evidently shapes the fecal pellets, which are twisted and have a deep spiral furrow in *A. subrugosa* (Fig. 25). In transverse section they show the coarse material irregularly positioned in a gelatinous coat. The pellets are about 2 mm long and 0.1 mm broad.

5. Glands of the alimentary tract

5a. Salivary glands. As in most Acmaeidae, there are 2 different pairs of salivary glands.

The anterior pair of *A. subrugosa* is asymmetrical in position and size. The right gland is broader than long and lies sideward and a little above the right esophageal chambers, together with the posterior salivary glands and just above the corresponding pleural ganglion. The left gland is longer than broad, is partially covered by the left esophageal chambers and the posterior salivary gland, and is almost entirely enclosed by the gonad. Both salivary glands (Fig. 8, SD) have long ducts which accompany the dorsal wall of the esophagus and open into the folds of the pharynx. The wall of the ducts consists of glandular cells and cubic ones with long cilia.

The posterior salivary glands are finger-shaped and open separately into the median esophageal chambers. They are coated with low, mainly mucous, glandular cells, and lined with cubic ciliary epithelium with few glands. The 2 layers of cells are separated by thick fibrous connective tissue.

5b. Digestive gland. The voluminous digestive gland is racemose, interweaving with the stomach and the intestinal loops, and also enclosing part of the radular sheath. It constitutes the principal portion of the visceral mass, except during reproduction, when the gonad enlarges.

As usual, there are 2 types of cells

in the hepatic tubules of *A. subrugosa*. The more numerous are the absorbing cells, which are cylindrical, up to $36\ \mu$ high, vacuolated and with basal fairly translucent nuclei; each apex is rounded and has a dense plasma. The secretory cells are placed at the angles of the tubules, stain intensely and appear in sections as triangles about $22\ \mu$ high.

The glandular cells rest on a basal connective layer which separates them from the blood lacuna. This basal layer is sometimes wanting, mainly in the region of the secretory cells, which in that case send out processes into the lacunae. The 2 cellular types also line the ducts of the gland, which gradually unite into a single channel. Shortly before its opening into the stomach, the channel is coated with columnar ciliary epithelium continuous with that of the stomach.

Circulatory system

1. Heart

The approximately triangular pericardium is at the left side at the back of the nuchal cavity in the 3 species. It is bounded on the left by the fore left portion of the columellar muscles and on the right by the gonad.

The heart consists of a triangular auricle and a ventricle, connected by wide transverse atrioventricular apertures. Numerous, variably strong muscle strings cross its lumen in various directions, giving it a fenestrate aspect. Only in *A. subrugosa* was a detailed study of this organ possible, but it is very similar in the other 2 species. The strings are especially numerous on the contiguous walls of the auricle and the ventricle. On the auricular side the atrioventricular aperture has a valve formed by a dorsal and a ventral lip fastened by slender muscular strings. These are more numerous on the ventral side and arranged at various levels. Their contraction opens the valve when the blood is forced from the auricle into the ventricle. On the ventricular side 2 thick muscular bands, originating

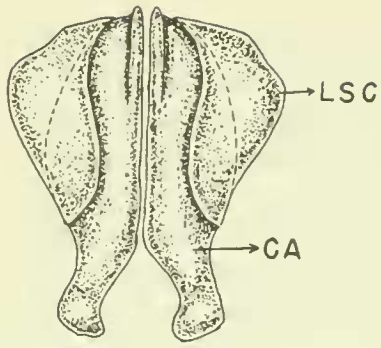
from many points on the left and right walls of the ventricle, are attached to the angles of the opening; their contraction closes the aperture during the ventricular systole.

The cavity of the ventricle communicates with the aorta by a long longitudinal gap in the midline of the right ventricular wall. The ventral lip of this gap functions as a valve; it is fastened to the ventral wall of the ventricle by short thin muscle strings, which open and close it during the ventricular systole and diastole, respectively. Dorsoventral muscle bands cross the circular opening through which the atrium receives the oxygenated blood.

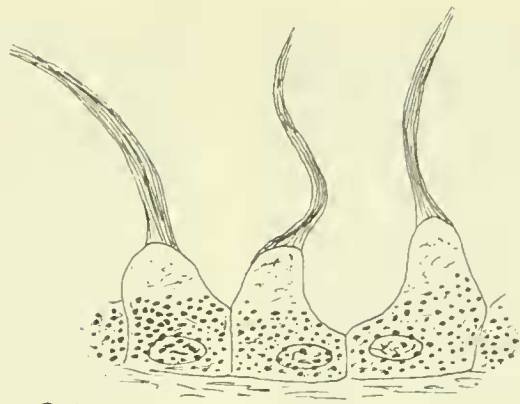
2. Arterial system

The aorta emerges from the right ventral side of the ventricle. Already at its origin, hence still within the pericardium, the aorta divides into an anterior and a posterior (visceral) branch. The anterior aorta attains the dorsal wall of the esophagus. It continues to descend, runs through the nervous visceral loop and under the right anterior salivary gland. Then it bends round the last right esophageal pouch, passes under the esophagus and over the radular sheath. It crosses the diaphragm, runs dorsally for a short extent along the radular sheath after having surrounded it completely. A little farther on, it sends backward a thin branch that passes immediately over the subintestinal branch of the visceral loop and supplies the hindmost part of the radular sheath.

The aorta bifurcates between the inner ends of the anterior cartilages of the odontophore. A pedal artery runs to the foot and a cephalic artery continues forward, still accompanying the radular sheath. In the median portion of the odontophore the radula pierces the dorsal wall of the cephalic artery, which a little farther on becomes lacunar and passes into the space of the cephalic (buccal) sinus (Fig. 8, CS) between the cartilages and the odontophoral muscles.



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24



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FIGS. 22, 24, 25. *Acmaea subrugosa*: 22, Odontophoral cartilages; 24, Epithelium of the right kidney; 25, Fecal pellets.

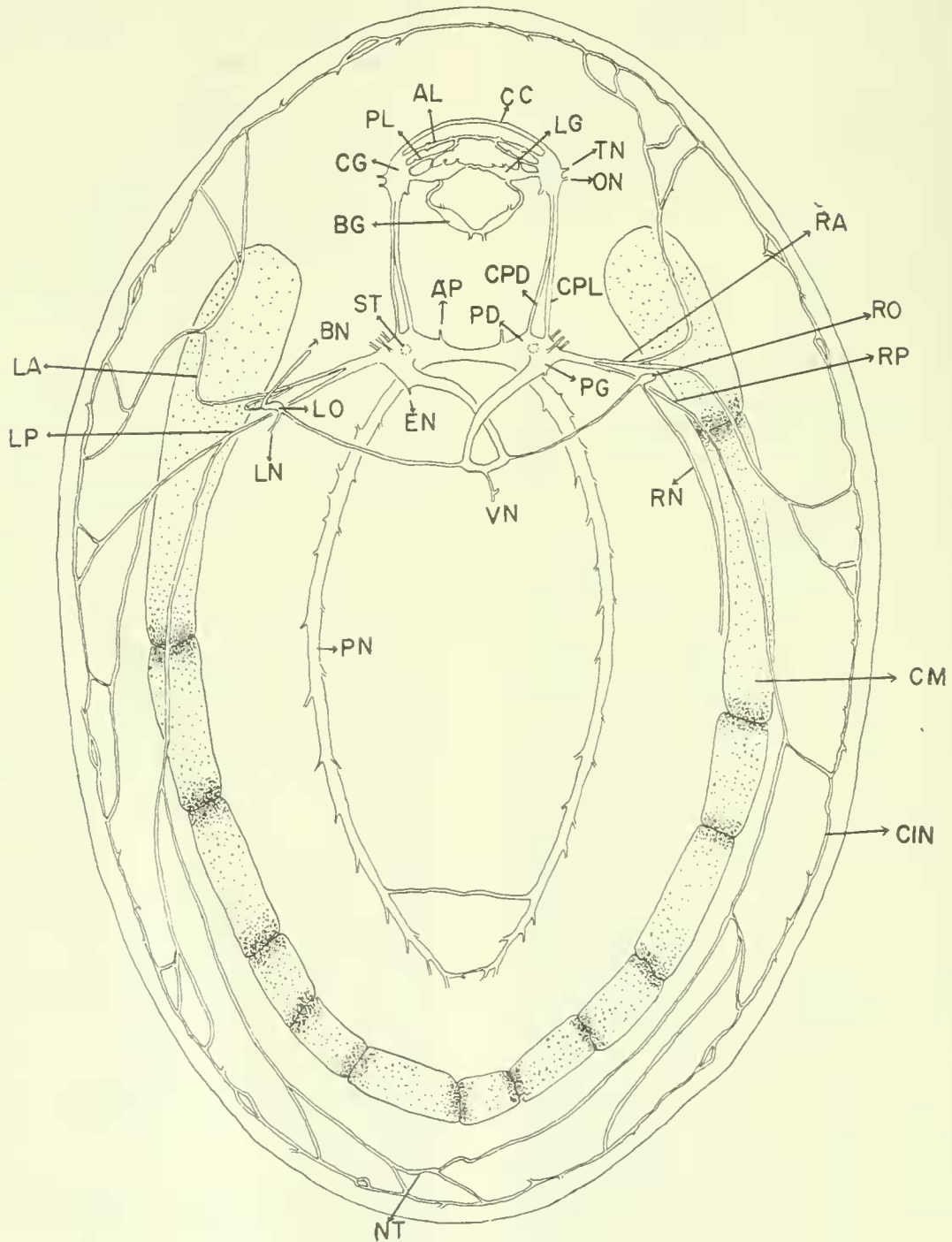


FIG. 23. *Acmaea marcusii*: nervous system.

The cephalic sinus makes up the broad anterior hemocoel, which supplies the head and the neck. It is separated from the visceral cavity by the diaphragm. This is a connective and weakly muscular membrane inclined downward and forward, so that the hindmost portion of the sinus is dorsal. The diaphragm is perforated dorsomedially by the esophagus, farther below by the aorta and the radular sheath, on either side by the salivary ducts and more ventrally by the branches of the visceral loop; finally, the extremity of the radular sheath pierces it on the right side. The cerebral ganglia and cerebropleural connectives are separated from the main cavity by connective-muscular bands. The bands form 2 small lateral pouches (Fig. 8) connected with the main cavity and with a space surrounding the labial ganglia by apertures in the walls and at the ends.

Some branches with little or ill defined walls arise from the cephalic sinus, extend into the lips and the tentacles, and along the pallial nerves, and pass into the pallial circulation. A little in front of the pedal ganglia and between the cerebropedal and pleural connectives, there are 2 large transverse gaps which lead blood from the cephalic sinus to the foot. They are lengthened backward, surrounding the pedal nerve cords as neural sinuses (Fig. 27, NS), named a median sinus by Willcox (1898: 436) and a neural artery by Fisher (1904: 24).

In *A. subrugosa* the pedal artery maintains its walls in the cephalic sinus and in its entire course through the foot. From the aorta it runs backward on the floor of the cephalic sinus, pierces the pedal muscle and divides, giving a thinner anterior and a thicker posterior artery. The former soon loses its individuality by branching into capillaries. The latter bifurcates under the pedal commissure, and its 2 branches (Fig. 27, PPA) run below the 2 sinuses which surround the pedal nerve cord. In *A. marcusii* the pedal artery ramifies before piercing the pedal muscle. The

neural sinuses accompany the posterior pedal commissure and coalesce. The 2 branches of the pedal artery unite in the same region but much deeper in the pedal muscle. After this junction the 2 pairs of vessels continue along the pedal cords. Nerves arising from these cords are supplied by the 2 vessels; the pedal artery remains farther below. The branches of the pedal artery are mostly directed to the lateral and inferior portions of the foot, whereas those of the neural sinuses supply the median and superior pedal portions and the columellar muscle.

The visceral aorta passes through the right posterior wall of the pericardium and, after a short descending course through the body cavity, penetrates the gonad and also attains the intestine and the digestive gland.

3. Venous system

The blood of the foot is drained by 2 systems. Small lacunae of the central portion open into the great medial pedal sinus (PS) that runs backward between the gonad and the foot, and communicates posteriorly with the renal blood system and still farther behind with the mantle vein. The other and more important system consists of the lateral pedal sinuses (LS), or vertical inter-fascicular vessel (Willcox, 1906: 184), which receive blood from the lateral and inferior portions of the foot. These sinuses are approximately 6 on each side in *A. subrugosa* and *A. marcusii*, but indistinct in the latter. They go upward through the columellar muscle, drain it, communicate laterally with the mantle vein and its branches, and centrally with the perivisceral lacuna, forming a T in cross-section. The blood that comes from the viscera goes in part to the broad perivisceral lacunae (PVL) which lie over the visceral mass; their cavity is crossed by numerous trabeculae of renal tissue.

The blood flows forward on both sides in the mantle vein (MV), whose slender cubic epithelium is underlain by a thin

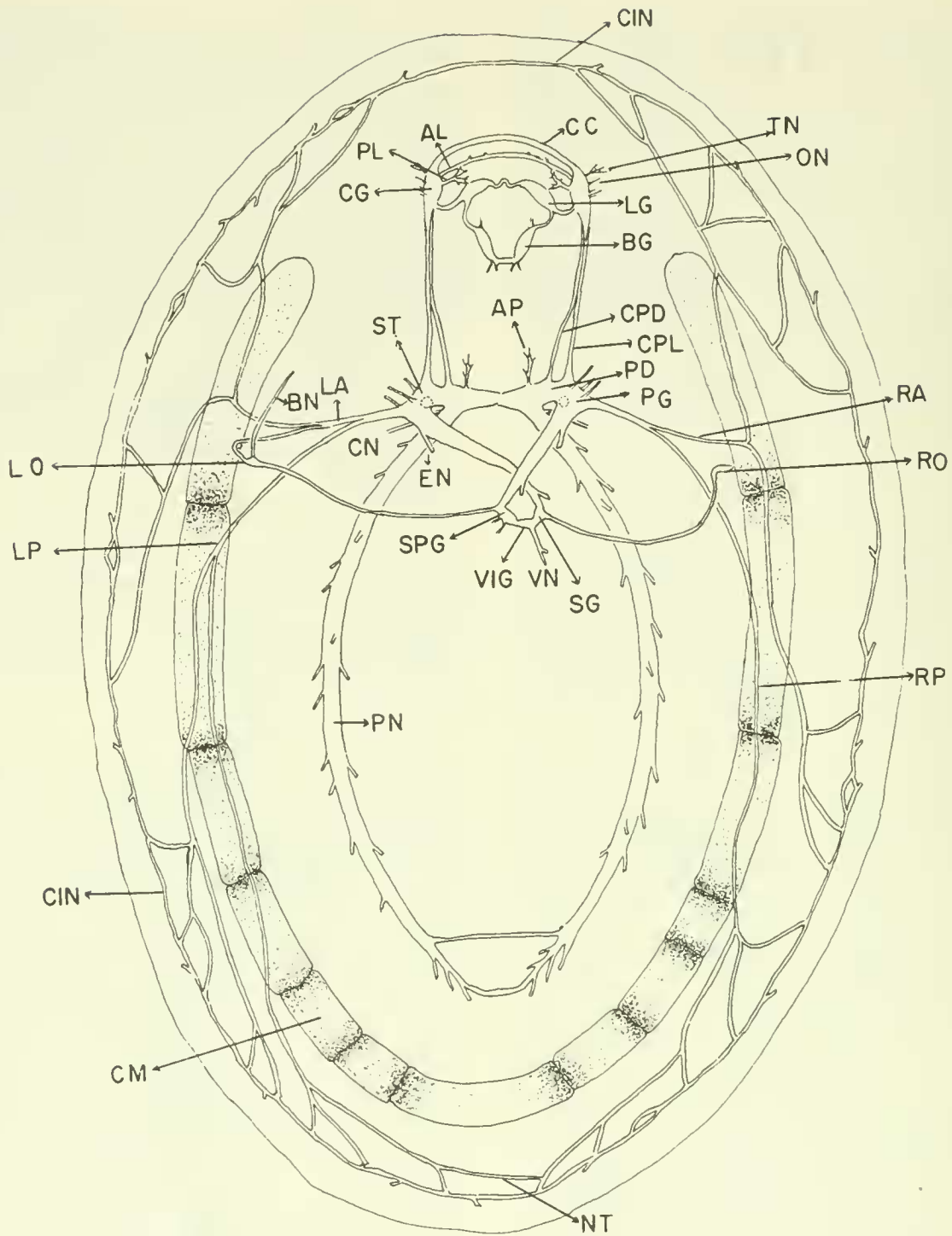


Fig. 26. *Acmaea subrugosa*: nervous system.

basal connective layer which is lacking in some regions. Oxygenated blood goes through the mantle arteries to the circumpallial sinus (CIS), where the blood runs forward on both sides. It is separated from the mantle vein by a longitudinal connective-muscular band traversed by the above-mentioned arteries. In the anterior region the mantle vein is connected with the intricate lacunar

system of the ceiling of the nuchal cavity, where the blood of the two previously-mentioned lacunae of the cephalic sinus also arrives. Thence, the blood flows chiefly to the circumpallial sinus. A small furrow accompanies the mantle vein. The epithelium of the furrow is a little higher than that of the lower face of the mantle, especially in *A. subrugosa* and *A. noronhensis*.

Part of the blood from the viscera goes to the rectal sinus, and then enters the afferent branchial vessel together with blood from the left kidney and anterior portion of the right. Thence it runs across the branchial leaflets to the efferent branchial vessel. The 2 branchial vessels communicate with one another through capillaries in the sustaining membrane of the branchial leaflet. The efferent branchial vessel passes through the posterior mantle wall and the pericardium and opens into the atrium; on its way it receives blood from pallial lacunae and especially from the circum-pallial sinus.

Nervous system

The following account refers chiefly to *A. subrugosa* and *A. marcusii* (Figs. 23, 26). The 2 egg-shaped cerebral ganglia (CE) lie on the anterolateral part of the buccal mass, at the bases of the tentacles. The cerebral commissure (CC) is broad; it runs over the odontophore. A thick anterior labial nerve (AL) arises a little under and in front of the base of the commissure. The 2 labial nerves descend and coalesce. In the upper lip the labial nerve forms numerous branches. A second and slenderer posterior labial nerve (PL) arises from the median inferior area of the ganglia, runs downward and attains the lateral portion of the lip where it ramifies; it anastomoses in front with a branch from the anterior labial nerve and in back with another one from the labial ganglia. Thus a circumoral nerve ring results. The thick tentacular nerve (TN), of dorsal origin, ramifies a little after entering the tentacle. The thin optical nerve (ON) arises immediately behind the tentacular nerve and goes directly to the eye.

The spindle-shaped labial ganglia (LG) lie under the posterior part of the sublingual cavity and are surrounded by the odontophoral muscles. They are connected by a sinuous commissure and send nerves toward the palps and the lower lip. The short cerebrolabial con-

nectives have some nerve cells which in *A. subrugosa* also extend backward and upward on the underside of the cerebral ganglia.

The stomatogastric system consists of 2 longish buccal ganglia (BG) between the radular sheath and the pharynx. They converge toward the commissure which lies behind. In front, the cerebrobuccal connectives slant forward, bend around the buccal mass and attain the posterior faces of the labial ganglia. Some fibers connect with the cerebral ganglia together with the cerebrolabial connective, others with the labial ganglia. A nerve emerges from the anterior portion of the buccal ganglia and accompanies the salivary ducts to the pharynx folds where it branches. Two other nerves (only one in *A. marcusii*) arise from the posterior end; the inner pair goes to the radular sheath, the outer one to the odontophore.

I did not find the subradular ganglia said to be characteristic of Acmaeidae (Fisher, 1904: 42). Neither did Willcox (1898) describe them in *A. fragilis*.

The cerebropleural (CPL) and cerebropedal (CPD) connectives arise from the posterior extremity of the cerebral ganglia. The former is thicker and begins farther outward and upward. They run backward along the lateroventral wall of the cephalic sinus. Cerebropleural and cerebropedal connectives, both with nerve cells, run parallel in their beginning; the latter diverge farther inward. Branches from these connectives innervate the lateral and inferior walls of the head. The static nerve begins within the cerebropleural connective, and separates from it at the point where the cerebropedal connective bends inward. The statocysts (ST) lie under the pleural ganglia.

The pleural ganglia (PG), outward from the tip of the odontophore, receive the cerebropleural connectives in front. As in *Patella* (Bouvier, 1887: 18; Davis & Fleure, 1903: 38), 2 pleural nerves go to the dorsolateral body wall, one arising together with the cerebropleural con-

nective, the other farther laterally; a third and thicker nerve accompanies the salivary gland and seems to innervate the anterior part of the columellar muscle. The pallial nerve runs backward and outward, branching into an anterior and a posterior nerve. In *A. subrugosa* and *A. marcusii* the right anterior pallial nerve (RA) enters the upper edge of the columellar muscle and bifurcates again into an anterior and a posterior branch. The former goes through the anterior portion of the muscle to the mantle, where it reaches the circumpallial nerve. The latter runs backward through the shell muscle and attains the mantle in the middle part of the body, subdivides and unites with the circumpallial nerve. The right posterior pallial nerve (RP) extends backward and upward between the kidney and the body wall, passing through the columellar muscle; in the posterior third of the body it traverses the mantle and reaches the circumpallial nerve. The left anterior pallial nerve (LA) bifurcates a little before it crosses the columellar muscle. Its posterior branch anastomoses with the osphradial nerve, and its anterior branch traverses the columellar muscle and bifurcates. The 2 branches run in opposite directions, crossing the mantle and coalescing with the circumpallial nerve. The left posterior pallial nerve (LP) runs, like the right one, between the kidney and the shell muscle, then passes through the muscle and finally branches. The 2 resulting nerves run backward across the muscle. The innermost attains the posterior third when it reaches the mantle, subdivides and coalesces with the circumpallial nerve. A small transverse nerve (NT) connects the 2 posterior pallial nerves as in *Lottia* (Fisher, 1904: 46) and *Patella* (Davis & Fleure, 1903: 38).

The circumpallial nerve (CIN) surrounds the mantle margin inside the gland ring. It receives the branches of the pallial nerves and sends out fibers to the mantle tentacles and ventral glands.

The esophageal nerves (EN) arise from the pleural ganglia together with the origin of the branches of the visceral loop. The left esophageal nerve is double, and its 2 components are joined, up to their middle, by a connective sheath. Then they separate and enter the ventral face of the esophagus, near the anterior salivary gland. The right nerve is single, quite small, and enters the right lateral wall of the esophagus in the region of the tubules of the posterior salivary gland.

The pedal ganglia (PD) lie a little under and in front of the pleural ganglia and are contiguous with them. In front they receive the cerebropedal connective and are united by a broad commissure, and the 2 anterior pedal nerves (AP) arise and enter the pedal muscle, branching extensively. The 2 ganglionic nerve cords are thicker; they run backward, and before entering the pedal muscle they emit outward and upward, into the body cavity and to the body wall, a branch (CN) that supplies the shell (columellar) muscle. The pedal cords are farthest from one another in the middle of the foot and converge backward, becoming united by a commissure. The terminal branches form another anastomosis. Peripheral branches, bending in sharp angles backward, go to the periphery, where they ramify especially over the girdle of glands. These nerves are not symmetrical and their number increases with growth; in the central and dorsal areas they are thinner and less numerous.

The visceral branches are broad and ganglionic, and hence are difficult to separate from the pleural ganglia. The hind part of the loop surrounds the aorta. A thicker nerve comes out from the supraesophageal branch, just over its crossing with the subesophageal branch, and goes backward to innervate the radular sheath. Near the subintestinal ganglion there arises a nerve which supplies the gut and the anterior portion of the right kidney. The connectives between the 3 concentrations of the vis-

ceral loop are so short that the ganglia are difficult to separate from one another. The suprintestinal ganglion is the first on the morphological left side; it lies over the right upper portion of the esophagus and gives origin to 3 nerves in *A. subrugosa*. The first, the only one in *A. marcusii*, is the ganglionic left osphradial nerve; it runs across the gonad, enlarging slightly under the osphradium, and forms the left osphradial ganglion (LO). Here it anastomoses with a previously-mentioned branch of the left anterior pallial nerve and sends forth the branchial nerve (BN) to the efferent branchial vessel. In *A. marcusii* it emits a left nephridial nerve (LN) behind the pericardium and the left portion of the right kidney. The other 2 nerves from the suprintestinal ganglion in *A. subrugosa* go to the heart, accompanying the anterior aorta dorsally and ventrally. The visceral ganglion is the hindmost ganglion of the loop. It sends forth only a voluminous nerve, the visceral nerve, that goes backward and to the left. It divides into an anterior and a posterior branch. The former runs to the rectum and the kidneys, and one of its subdivisions traverses the external wall of the afferent branchial vessel. At the tip of the ctenidium it joins the just described branchial nerve and, like this nerve, sends a fiber to each gill leaflet. The posterior nerve runs toward the organs of the visceral mass. Like the visceral ganglion, the subintestinal ganglion is covered by the right salivary gland; it only gives off the ganglionic right osphradial nerve, which in *A. subrugosa* is a little longer than the left one, and forms the right osphradial ganglion (RO). In *A. marcusii*, the right osphradial nerve sends backward the long right nephridial nerve (RN) which runs between the shell muscle and the right kidney, innervating it.

Sense organs

1. Tentacles

The surface of the tentacles is covered

with numerous papillae which increase the sensorial area; they are specially numerous on the inner face and the apex, and are absent on the dorsal surface. The longitudinal muscle fibers are united in bundles only along the inner face and so do not affect the shape of the eye during contraction; they partially surround a central mass of connective tissue with a dorsal vessel. The innervation was described above. The slightly cuticularized epithelium consists of cubic cells with sensory cells between them. Under the epithelium there are oblique distending muscles.

2. Eyes

The opening of the pear-shaped eyes is proportionally larger in young animals. The low cutaneous epithelium is higher in the area opposite the opening. The retinal cells in *A. subrugosa* are 20 μ high. The supporting cells of the retina (Fig. 21, SU) are bottle-shaped, cylindrical in 2/3 of their height, thinner in the upper third and dilated at the apex; their ovoid nuclei are hidden by granules of black pigment. The dumbbell-shaped sensory cells (SC) have basal nuclei and their apices project a little into the ocular cup. A gelatinous layer covers the retina. The connective tissue under the retina is formed by cells bulkier than those of other regions of the tentacle, and includes spacious blood lacunae.

3. Statocysts

The statocysts (Figs. 23, 26, ST) are egg-shaped and connected with one another by a fibrous ligament attached to the body wall. In *A. subrugosa*, the epithelium of the statocyst consists of cubic cells with broad nuclei and sensory cells with filamentous, sometimes branched processes.

The numerous statoconia have no growth lines.

4. Osphradium

The 2 yellowish semicircular papillae on either side of the floor of the

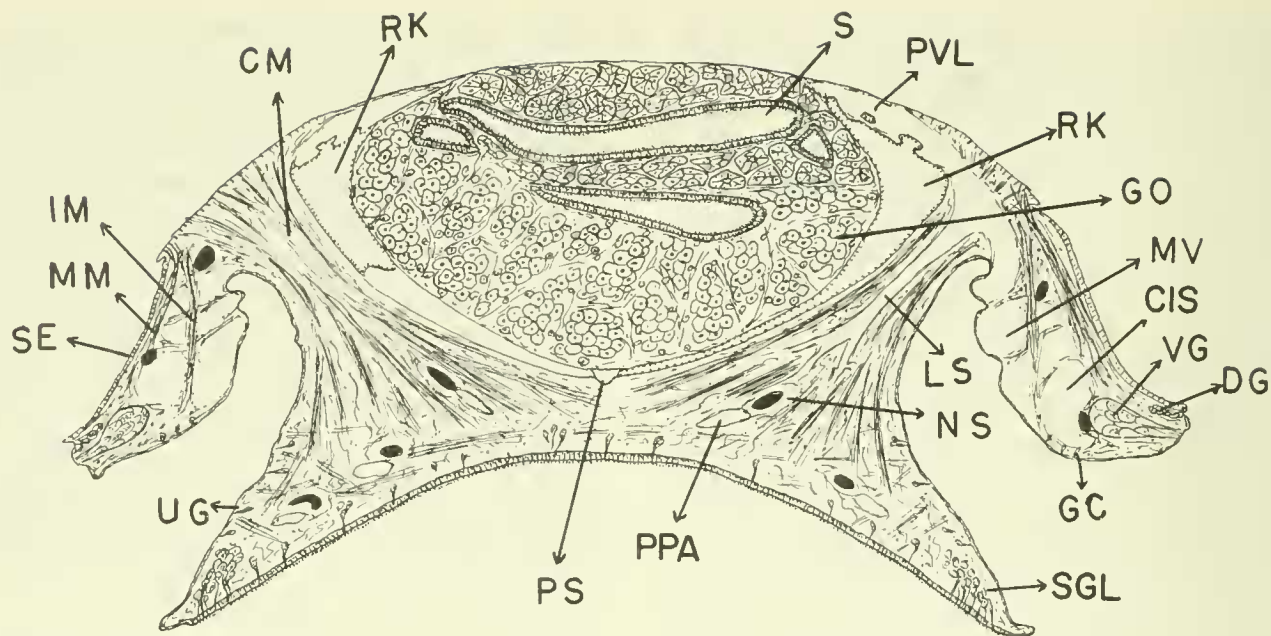


FIG. 27. *Acmaea subrugosa*: Cross-section of the median portion of the body.

nuchal cavity are like those in *Lottia* (Bernard, 1890: 225). They are made up of spongy connective tissue and coated with flattened epithelium. In *A. subrugosa*, cylindrical 10μ high cells cover the anterior, inner and postero-basal areas of the left papilla and the anterior and inner surfaces of the right one. There are 2 types of cells: supporting cells with an ovoid nucleus of loose chromatin, and neuroepithelial cells with a dense fusiform nucleus; the latter are connected with fibers coming from the osphradial ganglion. The sensory epithelium has the same position in *A. marcusi*, but is less developed on the right side. A band of cylindrical 12μ high epithelium, profusely ciliated and containing sensory cells, accompanies the branchial nerve from the ganglion to the pericardium and to the efferent branchial vessel. These 2 sensorial areas were already recognized by Thiele (1902: 327). According to Thiem (1917: 507), only the right one corresponds to an osphradium. In *A. testudinalis*, Yonge (1947: 466) considers as an osphradium a sensory area on a small protuberance over the osphradial ganglion, a little anterior to the left tubercle; on the right side he did not find an osphradial area. The 2

sensorial epithelia may function as osphradia because they are innervated by fibers of the same ganglion.

5. Pallial tentacles

Small tentacular prominences project at the margin of the mantle (Figs. 7, 8, PT). They consist essentially of connective tissue crossed by longitudinal muscle fibers; the low cylindrical epithelium contains some sensory cells. These are connected with branches of the circumpallial nerve. In *A. subrugosa* larger tentacles are situated near the circumpallial vessel; in *A. marcusi* they are quite small, and approximately equal in size, as in *A. testudinalis* (Fleure, 1904: 276).

Excretory apparatus

The kidney is similar in the 3 species. When the shell is removed, the right kidney (Fig. 27, RK) appears green owing to the color of the granules in its epithelium. It surrounds almost the whole visceral mass, ending at the left side together with the pericardium. It extends ventrally on the right to the median pedal sinus and on the left for $1/3$ of this extent. Small renal prolongations penetrate the peripheral interstices between the viscera. Dor-

sally the right kidney leaves free a little median area of digestive gland and gut. Small hollow trabeculae penetrate the perivisceral sinus, giving it a fenestrate appearance. This kidney has a large undivided lumen. At the right anterior side it ramifies, and its lower branch passes through the diaphragm, entering the cephalic sinus; the upper branch traverses the mantle, accompanying the rectum for a little extent, and opens on a large papilla at the inner end of the nuchal cavity together with the anus. This papilla is small in the male, and clothed with a high glandular epithelium in the females.

The small left nephridium lies in the mantle, dorsal to and to the left of the rectum. The opening near its anterior end is dorsal to the rectum, a little behind the anus; it has no papilla.

Willcox (1898: 439: *A. fragilis*) found only one kidney and considered it the originally left one, located mainly on the right side; topographically it corresponds to the right kidney of the species I studied.

The coating epithelium stands on a thin basal layer and is the same in both kidneys. It consists of 13.6μ high cells with ovoid basal nuclei (Fig. 24). In the middle and below, the plasma contains many green granules. The sometimes enlarged apex bears long cilia. The cells are specially numerous in the areas adjacent to the blood sinuses. Near the columellar muscle and the gonad the epithelium of the right kidney is flattened, 2μ high, and the nucleus is obscured by granules.

The wide renopericardial canal originates from the right side of the pericardium. Its epithelium is a continuation of the thin pericardial lining, and so the canal is difficult to follow. It goes to the right and forward, attains the lower face of the rectum, runs under the latter for a little way and then ramifies. The left branch gradually narrows, and opens through the left wall of the left kidney, showing a papilla formed by high ciliated cells near the nephropore. The right branch narrows, as is characteristic of the Acmaeidae; its

opening is imperceptible and does not form a papilla. A similar position and branching of the canal was described in several Patellacea. Willcox (1898: 440) identified the right renopericardial communication with a pore on the left anterior wall of the right kidney, adjacent to the pericardium.

Reproductive system

The 3 species are dioecious, without external sexual dimorphism. *A. fragilis* (Willcox, 1898: 441) is protandrous with a brief hermaphroditic period. According to Thorson (1935, in Fretter & Graham, 1962: 372), *A. rubella* is hermaphroditic. Thiem (1917: 589) did not find hermaphroditism in his Acmaeidae.

The size of the gonad varies with the season. When fully developed, the gonad (Fig. 27, GO) covers the viscera ventrally and laterally in both sexes. On its external surface it is in contact with the right kidney, except for a broad longitudinal band on the left apposed to the body cavity. In not quite mature animals it is possible to distinguish anteriorly a ventral, little developed right portion and a large left portion projecting dorsally at the posterior end of the nuchal cavity, between the pericardium and the rectum. This is the only part, visible when the shell is removed, which makes it possible to determine the sex without further dissection.

During growth, the ovocytes are fixed to trabeculae of the ovary by a short stalk through which they receive yolk granules. In *A. subrugosa* the eggs are released singly into water without mucous coat, as in *A. virginea* (Boutan, 1898: 1888). The eggs are generally light green, sometimes violet or brown. Their average diameter is 94.25μ ; their only cover is the vitelline membrane.

The spermatozoon of *A. subrugosa* is 15μ long, and has a conical head of 2μ . Animals with shells of 10 mm are sexually mature. On the coast of São Paulo reproduction is most intense in

August and September.

General remarks

The 3 families of the Patellacea — Lepetidae, Acmaeidae and Patellidae — cannot be arranged in an unequivocal genealogical tree. The Lepetidae have primitive characteristics in their shell (Dall, 1876: 247; 1893: 412), but are geologically much younger than the other 2 families. Their simple radula seem more reduced than primitive (Thiele, 1935: 1041). The ctenidium of the Acmaeidae may be an ancestral character (Yonge, 1947: 493; 1960: 108), but Thiele (1931: 38; 1935: 1081) considers it a novelty. The visceral loop of acmaeids is shorter and more concentrated, and hence farther advanced than in patellids. The Patellidae have a radula less different from the rhipidoglossate type, and hence in this respect seem more primitive than the Acmaeidae; in addition, they have an epipodial remnant.

The Patellacea apparently appeared in the Triassic (Knight et al., 1960: 231). According to Odhner (1923: 26, 31, 33), the Archhelensis hypothesis (v. Ihering, 1927: 7), the Continental Drift Theory (Wegener, 1929: 7) and that of Continental Bridges (Schuchert, 1932: 875; Willis, 1932: 917), the southern Atlantic Ocean is younger than the Pacific Ocean of the same latitudes. In so old a group as the Patellacea, the current preponderance of *Acmaea* in the old Pacific Ocean and that of *Patella* in the younger Atlantic cannot elucidate their evolution. The recent centers of specific radiation and those of origins may or may not coincide.

The anatomical differences (mandible, radula, course of the intestine) between the 3 Brazilian limpets I consider to be species characters. However, I studied few specimens only and compared the insular populations with only one mainland population. Inter- or intra-population variation could exist along the Brazilian mainland coast. It is unknown whether the 3 Brazilian species have

free-swimming larvae, such as those of *A. virginea*, studied by Boutan (1898, 1899).

I consider shell characters in the 3 species to be less important than anatomical characters, because the close contact of the shell with the environment makes ecological variation probable. The radula seems to offer good specific characters in the number and form of denticles. Test (1946: 5) prefers to separate species by the basal ribbon; using this character, I did not arrive at definite conclusions with regard to distinguishing my species. The analysis of the course of the intestine, proposed by Haller (1894), was taken up by Fleure (1904: 280), who established relationships among the genera of the Docoglossa. I have used this character and the shape of the mandible for the first time to distinguish species of *Acmaea*.

Differentiation of the 3 allopatric species does not seem to be old. The volcanic island of Trindade arose in the Upper Pliocene (3.3 million years ago) and the island of Fernando de Noronha, also volcanic, in the Middle Pliocene (9 million years ago). This information was kindly given me orally by Dr. Umberto Cordani (Department of Geochronology, Universidade de São Paulo).

DIAGNOSIS OF *ACMAEA MARCUSI* SP. N.

Shell solid, conic, with ovate base. Apex directed forward, height variable, periostracum usually eroded. Shell produced at its ends, with high, thin radial striae. Fully-developed limpets (9 specimens) average 18.5 mm in length, 7.3 mm in height and 15 mm in greatest breadth. Color light brown, sometimes with white axial bands. A zone of radial dark brown bands along the inner margin, sometimes so numerous that they form a dark, almost continuous band. Columellar scars nacreous and almost imperceptible, with a narrow inner dark brown band limiting an innermost leaden surface from the whitish peripheral area.

Jaw slender, narrow, strongly concave anteriorly, widened and flattened backward, its thicker foremost third separated by a transverse furrow. Radula characterized by convergent inner edge of the 2 symmetrical second lateral teeth.

Holotype, a complete limpet in the collection of the Museu Nacional, Rio de Janeiro, No. 3,200; further specimens in the Departamento de Zoologia, Secretaria da Agricultura, Estado de São Paulo.

Named after Prof. Dr. Ernst Marcus.

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RESUMEN

SOBRE LAS ESPECIES BRASILEÑAS EN EL COMPLEJO
DE *ACMAEA SUBRUGOSA*

Las lapas marinas, *Acmaea subrugosa* d'Orbigny, 1841, *A. noronhensis* E. A. Smith, 1890, y *A. marcusii* n. sp. son descritas en el presente trabajo. La primera se distribuye en la costa continental de Brasil, desde Alagoas hasta Rio Grande do Sul y también en Uruguay; la segunda de la Isla de Fernando de Noronha, y la tercera de la Isla de Trindade. Estas especies no se pueden distinguir consistentemente por la concha. Sin embargo, presentan diferencias en la mandíbula (Figs. 9-11), rádula (Figs. 12-14), tracto intestinal (Figs. 15-17) y algunos nervios periferales.

АБСТРАКТ

О БРАЗИЛЬСКИХ ВИДАХ ИЗ ГРУППЫ *ACMAEA SUBRUGOSA*
(GASTROPODA, PROSOBRANCHIA, PATELLACEA)

Гильберто Риги

Описываются морские блюдечки *Acmaea subrugosa* d'Orbigny, 1841, *A. noronhensis* E. A. Smith, 1890 и *A. marcusii* sp. n. Первое отмечается для побережья Бразилии, от Алагааса до Рио-Гранде-до-Сул и для берегов Уругвая; второе - для о. Фернандо-де-Норонья и третье - для о. Тринидад. Они не могут быть достоверно определены по их раковинам. Однако, они различаются по мандибуле (рис. 9-11), радуле (рис. 12-14), топографии кишечника (рис. 15-17) и некоторым периферическим нервам.